The proximate basis of inter- and intra-population variation in female plumage coloration in the House Finch

GEOFFREY E. HILL

Department of Biology, Queen's University, Kingston, Ont., Canada K7L 3N6

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As in many sexually dichromatic species in which males are brightly colored, female House Finches (*Carpodacus mexicanus*) show a subdued expression of the same coloration as males. I quantified the carotenoid plumage coloration of females from the subspecies *C. m. frontalis* in Michigan, New York, Hawaii Island, and two sites in California, and from the subspecies *C. m. griscomi* in Guerrero, Mexico. The proportion of females with detectable carotenoid pigmentation differed significantly among populations, as did the median plumage brightness of colorful females. In Michigan, but not California, yearling females tended to be more colorful than older females. Among *C. m. frontalis* populations, there was a significant positive correlation between the plumage brightness of females and males, but in the *C. m. griscomi* population males were brightly colored while females were drab. In aviary experiments, females of all ages and from all populations converged on a similar plumage brightness after molt when fed a common diet. Moreover, females from all populations showed maximum color expression when provided with abundant red carotenoid pigments. These observations suggest that local and regional variation in the plumage brightness of females reflects local and regional variation in the availability of dietary carotenoid pigments and that female House Finches do not actively forage for carotenoids.

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Comme chez plusieurs espèces dichromatiques chez lesquelles les mâles sont brillamment colorés, les femelles du Roselin familier (*Carpodacus mexicanus*) exhibent une version atténuée de la coloration des mâles. Il a été possible de mesurer quantitativement l'intensité de la coloration caroténoïde des femelles chez les sous-espèces *C. m. frontalis* du Michigan, du New York, de l'île d'Hawaï et de deux sites de Californie, et *C. m. griscomi* de Guerrero au Mexique. Le pourcentage de femelles qui possédaient une coloration caroténoïde détectable variait significativement d'une population à une autre; il en allait de même de l'éclat du plumage des femelles les plus colorées. Au Michigan, mais non en Californie, les femelles d'un an avaient tendance à être plus brillamment colorées que les femelles plus âgées. Chez les populations de *C. m. frontalis*, l'éclat du plumage des femelles montrait une corrélation positive significative avec celui des mâles, mais chez la population de *C. m. griscomi*, les mâles avaient beaucoup d'éclat, alors que les femelles étaient ternes. Dans une expérience en volière, des femelles de tous les âges et de toutes les localités avaient tendance à développer un plumage d'éclat semblable après la mue lorsqu'elles étaient nourries d'une même diète. De plus, les femelles de toutes les populations exhibaient le plumage le plus éclatant lorsque leur diète contenait d'abondants pigments caroténoïdes rouges. Ces observations laissent croire que les variations locales et régionales dans l'éclat du plumage des femelles dépendent des variations locales et régionales dans la disponibilité de pigments caroténoïdes et que les femelles se nourrissent passivement de ces pigments.

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Introduction

Bird species that display colorful plumage are generally classed as sexually monochromatic or dichromatic (e.g., Rohwer and Butcher 1988). In many dichromatic species, however, the less ornamented sex (hereafter assumed to be females) shows a subdued form of the same color pattern displayed by the more ornamented sex. Thus, there actually exists a continuum from equal ornament expression in both sexes to no expression in females. Moreover, the expression of female ornamentation can vary substantially among individual females within a population (e.g., Red-winged Blackbirds, *Agelaius phoeniceus*; Payne 1969; Miskimen 1980*a*, 1980*b*; Black-headed Grosbeak, *Pheucticus melanocephalus*; Hill 1988), and among populations within a species (e.g., Wilson's Warbler, *Wilsonia pusilla*; Pyle et al. 1987). Research on the function and proximate control of plumage coloration has focused almost entirely on males (see Brush 1978; Butcher and Rohwer 1989 for reviews). Expression of ornamental coloration in females in dichromatic species has generally been viewed as a correlated response to selection for the character in males (Lande 1980; Payne 1984), but little empirical research has been conducted on either the evolutionary or proximate control of such female coloration (but see Miskimen 1980*a*, 1980*b*; Muma and Weatherhead 1989, 1991).

In this study, I examined the proximate basis of variation in female plumage coloration both within and among populations of the House Finch (*Carpodacus mexicanus*), a dichromatic passerine species. House Finches are native to western North America, from southern British Columbia to Oaxaca, Mexico (Moore 1939; American Ornithologists' Union 1983). Populations of House Finches derived from birds captured in coastal California were also introduced to the eastern United States in 1940 (Elliot and Arbib 1953) and to the Hawaiian Islands around 1870 (Grinnell 1911). Within all populations of House Finches, males display coloration ranging from pale yellow to bright red on their crown/eyestripe, throat/breast, and rump (Grinnell 1911; Michener and Michener 1931; Hill 1990, 1992, in press). In a study of geographic variation of male coloration (Hill 1993*b*), I also found that populations of House Finches from California, Hawaii, Michigan, and New York belonging to the subspecies *C. m. frontalis* vary substantially in the mean plumage brightness of males. In addition, males from the subspecies *C. m. griscomi* sampled in Guerrero, Mexico have much less extensive ventral coloration (patch

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size) than *frontalis* males from any population (see Moore 1939; American Ornithologists' Union 1957; Hill 1993*b*, for additional details of subspecies taxonomy and male coloration).

Some female House Finches also show ornamental coloration of the same plumage regions as males (McEntee 1970), but it is never as intense as that of males and is highly variable. Many females are entirely drab, with no red, yellow, or orange coloration; some show coloration ranging from faint yellow to fairly intense red only on their rump; and a few display both rump coloration and a wash of coloration on their breast and crown (McEntee 1970). In all cases, the coloration of female House Finches is overlain on a heavy pattern of melanin pigmentation (Moore 1939; personal observation) that is lacking in males. Virtually no information on geographic variation in the plumage coloration of female House Finches has been published.

The colorful plumage of both male and female House Finches is a result of carotenoid pigmentation (Brush and Power 1976; Hill 1992, 1993*b*). It is well known that birds cannot synthesize carotenoid pigments and must obtain them from their diet (Goodwin 1950; Brush 1978, 1990). It has previously been shown that variation in male House Finch coloration both within (Brush and Power 1976; Hill 1992) and among populations (Hill 1993*b*) is a consequence of individual variation in the intake of carotenoid pigments rather than intrinsic differences among individuals in the ability to display coloration. Therefore, it seemed likely that diet, and particularly the intake of carotenoid pigments, must play a significant role in determining the expression of plumage coloration in female House Finches as well. In addition, McEntee (1970) suggested that yearling female House Finches tend to be more colorful than older females, so I also tested the effect of age on the expression of female coloration. I sampled females in wild populations of House Finches to quantify variation in expression of female plumage coloration both within and among populations, and I conducted feeding experiments with captive females to test the effect of age and diet on color expression. Ultimately, my goal was to provide a better framework for understanding the evolution and maintenance of ornament expression in females of dichromatic species.

Methods

Scoring plumage brightness

I scored the plumage coloration of females following the same general protocol that I used for scoring males (Hill 1990, 1992). Color, as it is perceived by humans, and presumably birds, is a result of the interaction of hue, intensity, and tone (Kornerup and Wanscher 1983). Thus, to describe fully the color of an object, one must place it in the three-dimensional axis system formed by these variables. In addition, plumage coloration varies across the surface of House Finches, so an overall plumage score must account for variation among plumage regions.

I recorded the coloration of six plumage regions (three areas on the underside, plus the crown, eyestripe, and rump) as a separate hue, intensity, and tone score based on comparison with color chips in the *Methuen Handbook of Colour* (Kornerup and Wanscher 1983). The lowest ventral plumage region that I used in scoring males (see Hill 1992) was not included in my analysis of female coloration because *griscomi* males and females lack carotenoid pigmentation in this lower ventral region, and including the lower region would artificially deflate the scores of *griscomi* females (see Hill 1993*b*). As in males, female hue scores ranged from no carotenoid pigmentation (1) through yellow (ca., 2–4) and orange (ca., 5–8) to red (ca., 9–10). The intensity or chroma of the coloration of female plumage ranged from 1 to 5 (very little color present to fairly intense coloration) and the tone or value ranged from 1 to 5 (from brown to purer coloration). I then added the 18 scores to derive a single index value that I used as an estimate of overall plumage brightness (see Hill (1990, 1992) for additional details). Because of the way in which I set up the plumage variables (with higher scores corresponding to brighter plumage), adding plumage scores to derive an index value and collapsing scores into principal components yielded very similar results; the correlation coefficient between PC1 and my additive plumage index was 0.99. I used index values instead of PC1 values in my analyses because index values (positive integers) were easier to work with.

TABLE 1. Number of female House Finches sampled at different locations and dates

Site	Location N lat.	Location W long.	Date	Number captured
Michigan				
Ann Arbor	42°10′	83°40′	February–July, 1988–1990	415
New York				
Yaphank	40°50′	72°54′	December 1989	13
Eastport	40°40′	72°40′	December 1989	25
California				
Alviso	37°20′	121°55′	February 1990	56
San Jose	37°21′	121°58′	February 1990	26
Hawaii				
Pohakuloa	19°45′	155°33′	January 1989	23
Guerrero, Mexico				
Omiltemi	17°30′	100°50′	January 1990	8
Chilpancingo	17°33′	99°30′	January 1990	21

Population studies

I studied a breeding population of House Finches on the main campus of the University of Michigan, Ann Arbor, from 1988 to 1991. I trapped House Finches at feeding stations and marked individuals with unique combinations of colored leg bands. Whenever possible, I scored the plumage coloration of females once each year between February and July. In age comparisons, "yearling" females were banded either as nestlings or in juvenile plumage (as diagnosed by wide buffy edges to the tertials and secondaries; personal observation) in the previous year, and "ASY" (after second year; 2 years old or older) females were present in adult plumage for at least a second breeding season. I did not record female plumage coloration in 1988, but I used 1988 observations to age individuals. In each of the 4 years of this study, approximately 70% of females within the study area were banded.

I also captured female House Finches at the Coyote Creek Riparian Station in Alviso, California between 11 and 13 February 1990. Many of the birds that I captured at Coyote Creek had been banded previously, so the ages of many of the females could be determined from records at the banding station.

Geographic comparisons

I sampled *frontalis* females in New York, Michigan, California, and Hawaii Island, and *griscomi* females in Guerrero, Mexico. In New York, California, and Mexico I also sampled two local populations separated by at least 12 km. All sampling was conducted between December and February, except in Ann Arbor, Michigan, where sampling was conducted between February and July. Table 1 summarizes sample locations and dates and the number of females examined.

Feeding experiments

I captured House Finches for captive flocks in Hawaii in 1989, California and Guerrero in 1990, and southeastern Michigan in both 1989 and 1990. Michigan females were used in feeding experiments in both 1989 and 1990, but Hawaiian females were used only in 1989, and California and Guerrero females only in 1990. Whenever possible, Michigan females were aged at the time of capture by plumage pattern (July and August), or by examining their skulls for the extent of pneumatization (September through November); females from other populations were captured too late in the year for age to be determined. Finches were housed in unisexual flocks in large flight cages (2.5 × 2.5 × 4 m) on the roof of the Museum of Zoology on the University of Michigan campus. All birds were provided with water treated with "8-in-1 Vital-sol" multivitamins, and they were fed a basic diet of oil sunflower seed and "Kaytee Wild Finch Food" (Kaytee Products Inc., Chilton, Wisconsin) which contained (by weight) canary seed (33%), niger seed (20%), rape seed (12%), finch millet (10%), white millet (10%), red millet (5%), flax (5%), and calcium granules (5%). Seed was provided *ad libitum* by placing it in hanging feeders.

In 1989, I divided 25 females from Michigan and 20 females from Hawaii into two flocks that I housed in separate flight cages. I fed females in one flock (composed of 19 Michigan and 10 Hawaiian females) the basic diet plus chopped apples coated with canthaxanthin (Roxanthin Red 10 WS, Hoffmann-LaRoche; approximately 0.01 g/g apples) and water treated with the same (approximately 0.001 g/mL water). Canthaxanthin is a red carotenoid pigment not found in the plumage of wild House Finches but which is readily used by males to pigment their plumage (Brush and Power 1976; Hill 1992, in press). I fed females in the second flock (composed of 6 Michigan and 10 Hawaiian females) the basic diet plus untreated water and apples. In 1990, I divided females from Michigan, California, and Guerrero into two groups. One group (composed of seven Michigan, nine Californian, and six Guerrero females) was fed the basic diet with canthaxanthin added to their water (Roxanthin Red 10 WS, Hoffman-LaRoche, approximately 0.001g/mL water); the other group (composed of three Michigan, eight Californian, and six Guerrero females) received the same diet with untreated water. I scored the plumage of all females on the controlled diet before and after molt.

Statistical analysis

The distribution of plumage scores of female House Finches in all populations was highly skewed, with a preponderance of individuals displaying no detectable carotenoid coloration. Consequently, simple comparisons of means or median scores among populations were not informative. Instead, I used a Kolmogorov–Smirnov test to compare the distribution of scores among populations. After testing for differences in the distribution of plumage scores, I used a χ^2 test to determine whether the proportion of females with detectable carotenoid coloration differed among populations, and I used a Kruskal–Wallis test to compare the scores of females that showed detectable carotenoid coloration. Comparison among populations in different geographic areas entailed a total of 10 tests, so I adjusted the α for rejecting the null hypothesis following Rice (1989).

The distribution of color types among most groups of captive females was much less skewed. Only pretreatment groups had many females with no coloration, and I analyzed data from these groups exclusively using a Wilcoxon match-paired sign-ranks test (comparing pretreatment scores to the scores of the same individuals after treatment). With such a match-paired test, the distribution of pretreatment female plumage scores did not affect comparisons. Nearly all females in posttreatment groups showed some detectable carotenoid coloration, so I was able to compare the median plumage brightness scores of females in different treatments of feeding experiments using a Mann–Whitney *U*-test for paired comparisons and a Kruskal–Wallis test for multiple comparisons. In cases where a Kruskal–Wallis test indicated significant differences among populations, I used *a posteriori* paired-comparisons to see which populations differed significantly (Siegel and Castellan 1988).

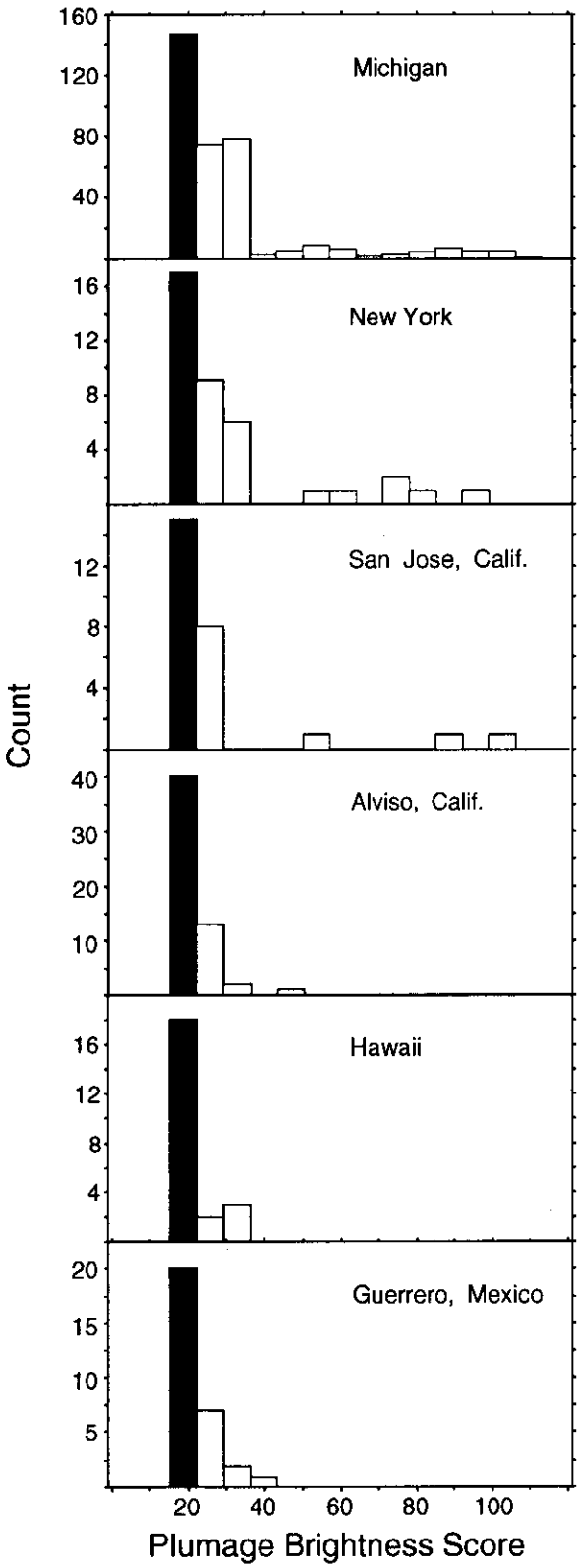

FIG. 1. Frequency distributions of plumage brightness scores of female House Finches sampled in different populations. The black bars represent females with no detectable carotenoid pigmentation. See text for details of the plumage scoring technique and Table 1 for collecting sites.

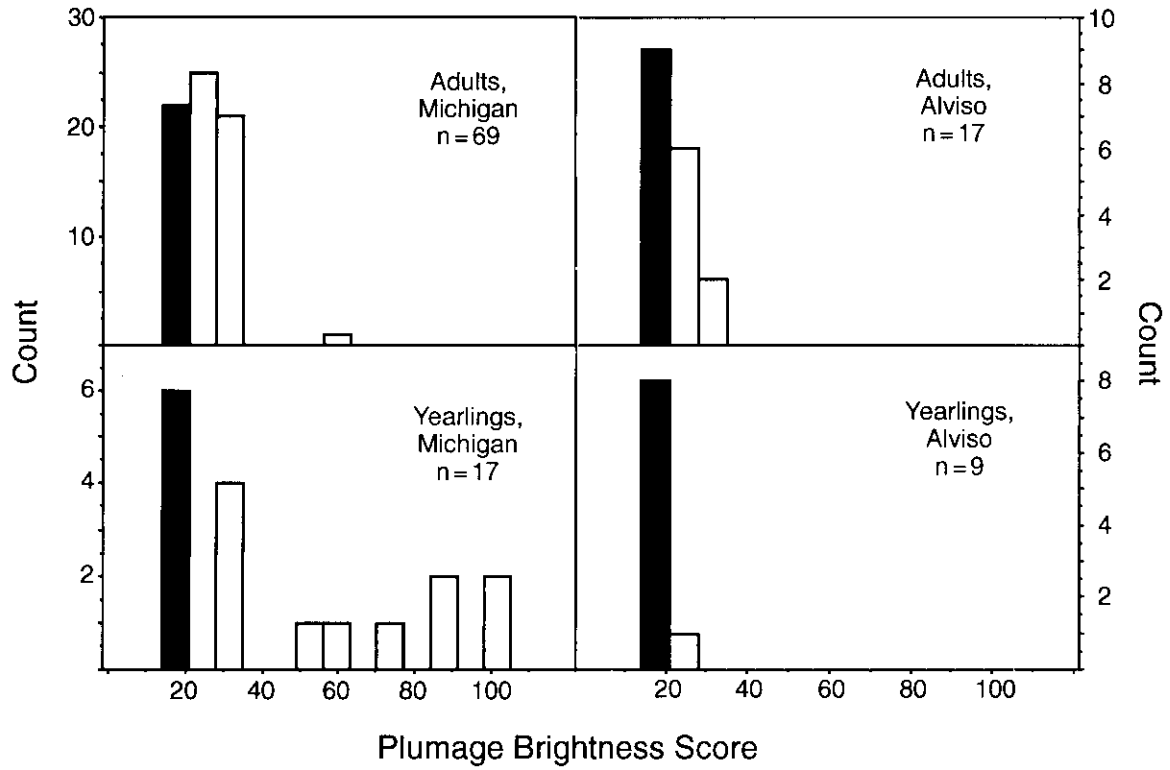

FIG. 2. Frequency distribution of plumage brightness scores of known-age female House Finches captured in Ann Arbor, Michigan, and Alviso, California. The vertical black bars represent females with no detectable carotenoid pigmentation. See text for details of the plumage scoring technique.

TABLE 2. Aspects of carotenoid plumage coloration of female House Finches from different populations

Population	*n*	Proportion with coloration: present	Proportion with coloration: absent	Brightness score[a]
Michigan	415	0.564	0.436	39.0±1.5
New York	38	0.553	0.447	41.5±4.8
Michigan and New York	453	0.563	0.437	39.4±1.3
San Jose, Calif.	26	0.423	0.577	42.3±8.5
Alviso, Calif.	56	0.286	0.714	28.2±1.0
Hawaii	23	0.217	0.783	29.4±3.1
Guerrero, Mexico	29	0.345	0.655	28.5±1.2

[a]Mean (±SE) plumage brightness scores of females with some detectable carotenoid pigmentation.

Results

Microgeographic variation

I found no differences between local populations in New York or Guerrero, either in the proportion of females with detectable carotenoid pigmentation (New York: $\chi^2 = 0.02$, df = 1, $P = 0.89$; Guerrero: $\chi^2 = 0.05$, df = 1, $P = 0.82$), or in the median plumage scores of females with carotenoid pigmentation (New York: $z = 1.52$, $P = 0.13$; Guerrero: $z = 1.03$, $P = 0.30$; Mann–Whitney *U*-test), so I pooled data from sites within these regions. I also found no significant differences in the proportion of colorful females ($\chi^2 = 0.02$, df = 1, $P = 0.89$) or in the median plumage score of females displaying coloration ($z = 1.22$, $P = 0.22$; Mann–Whitney *U*-test) between populations in Alviso and San Jose, California. However, females in these populations showed the same pattern of relative plumage brightness as males: the San Jose population had a higher proportion of females displaying carotenoid coloration and a higher mean score of colorful females than did females sampled 12 km away in Alviso (Fig. 1; Table 2). Because of the large difference in mean coloration observed in males from these populations (Hill 1993*b*), I treated females sampled in Alviso and San Jose separately in interpopulation comparisons.

Females sampled in New York and Michigan were very similar in the proportion of individuals with detectable carotenoid pigmentation ($\chi^2 = 0.001$, df = 1, $P = 0.97$), as well as in the median plumage brightness of females with carotenoid pigmentation ($z = 0.58$, $P = 0.56$; Mann–Whitney *U*-test; Fig. 1; Table 2). The similarity of females in these two eastern U.S. sampling sites is in accord with the similarity of male plumage brightness in these populations (Hill 1993*b*). So, to increase the power of the multiple-comparisons test I pooled data from New York and Michigan.

Geographic variation

A large proportion of females in all populations showed no detectable carotenoid coloration (Fig. 1; Table 2) and the distribution of plumage scores did not differ between populations ($P > 0.05$ for all paired comparisons; Kolmogorov–Smirnov tests). However, the proportion of females that displayed some plumage coloration was significantly greater in Michigan and New York than in either Hawaii or Alviso ($\chi^2 = 9.20$, df = 1, $P < 0.02$ and $\chi^2 = 14.29$, df = 1, $P = 0.002$, respectively; Fig. 1; Table 2). The median brightness score of females that displayed some coloration was also higher for populations in Michigan and New York than for those in

Alviso or Guerrero (H = 13.44, df = 5, P = 0.009; Kruskal–Wallis test with *a posteriori* paired-comparisons; Fig. 1; Table 2). Other populations did not differ significantly in either the proportion of females with coloration or the median plumage brightness of females with coloration (Fig. 1; Table 2).

Age effects

The effect of age on expression of female plumage coloration varied among populations. In southeastern Michigan I found that the proportion of females with detectable carotenoid coloration was similar in ASY and yearling age groups (χ^2 = 0.09, df = 1, P = 0.76) as was the distribution of color types (z = 1.47, P = 0.14; Kolmogorov–Smirnov test; Fig. 2). However, yearling females in southeastern Michigan with detectable carotenoid coloration had significantly higher plumage brightness scores than the ASY females with carotenoid coloration (z = 4.08, P = 0.0001; Mann–Whitney U-test; Fig. 2). I found no effect of age on color expression in Alviso, California: ASY and yearling females did not differ in the distribution of color types (z = 0.87, P = 0.38; Kolmogorov–Smirnov test), and they were alike in the high proportion of females in both age groups that displayed no detectable carotenoid coloration (χ^2 = 0.16, df = 1, P = 0.16; Fig. 2). Only one yearling female in the California sample showed detectable carotenoid pigmentation, so I could not compare the brightness scores of ASY and yearling females with carotenoid coloration.

Using data from the Michigan population, I investigated the degree to which individual appearance changed between years, and the effect of age on annual plumage change. I recorded the plumage coloration of 31 females in consecutive years, including three birds known to be yearlings, and nine birds known to be ASY in year 1 of the comparison. I found a significant correlation between the plumage brightness scores of individuals between years (z = 2.89, n = 31, P = 0.004; Spearman rank-order correlation coefficient), with no tendency for individuals to become brighter or drabber between years (P = 0.50; sign test; Fig. 3). When I repeated these analyses for a small sample of adult females, I found a nearly significant correlation between the plumage brightness scores of individuals between years (z = 1.82, n = 9, P = 0.07; Spearman rank-correlation coefficient) and no tendency for individuals to become brighter or drabber (P = 0.33; sign test; Fig. 3). Few conclusions could be drawn from data on only three yearling females, but the only individual with brightly colored plumage in year 1 decreased substantially in plumage brightness between years (Fig. 3).

Feeding experiments

In both years, and for all treatments, females from all populations converged on a similar appearance after molt on a standardized diet (Fig. 4). In 1989, when they were maintained on a diet supplemented with canthaxanthin, females from both Hawaii and Michigan grew red feathers approaching maximum color expression for females, with no significant difference in plumage brightness scores between the two groups (z = 1.38, P = 0.17; Fig. 4). The post-treatment plumage brightness scores of both Hawaiian and Michigan females were significantly greater than their corresponding pretreatment scores (Hawaiian: z = 2.80, P = 0.005; Michigan: z = 3.72, P = 0.0002; Fig. 4). When they were maintained on a carotenoid-deficient diet of plain seeds, most females from both Hawaii and Michigan grew feathers with a wash of yellow coloration on their rump and breast. Again, there was no significant difference between females from the two populations in plumage brightness scores (z = 0.16, P = 0.87; Fig. 4). There were also no differences between the pre- and post-treatment plumage scores of Michigan females (z = 0.31, P = 0.75; Fig. 4), but Hawaiian females increased significantly in carotenoid coloration after molt on a plain seed diet (z = 2.67, P = 0.008; Fig. 4).

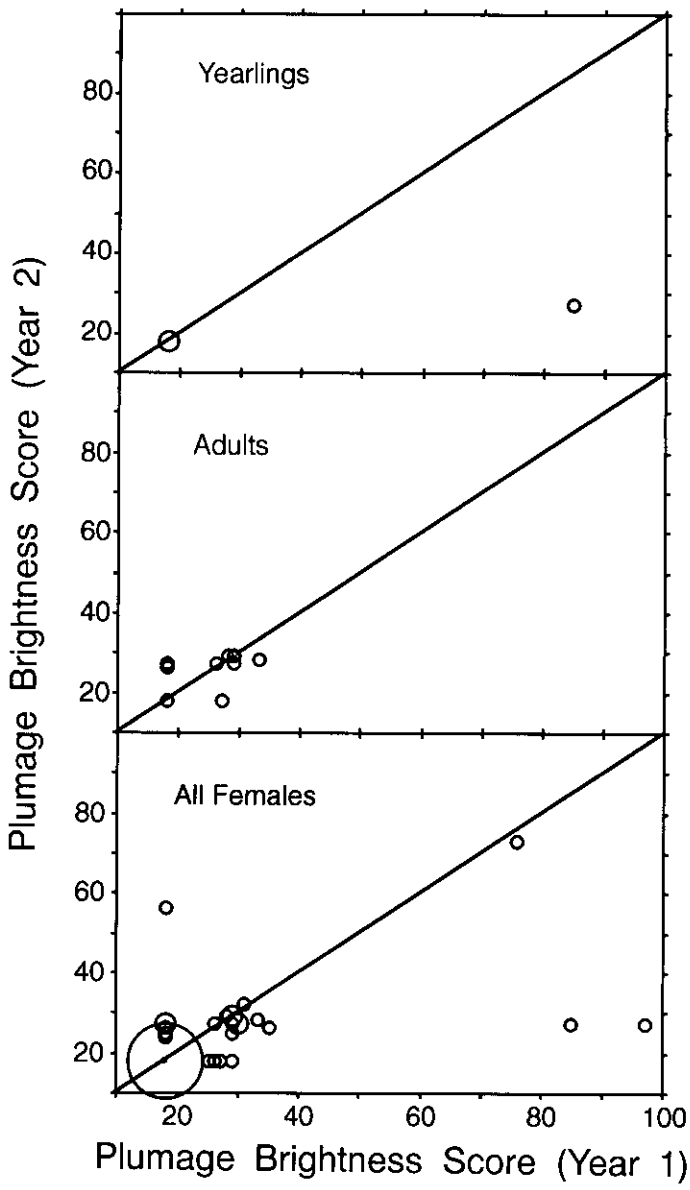

FIG. 3. Between-years change in individual plumage brightness of females. Stated ages are in year 1 of the comparison. The isometric line (slope = 1) is indicated. See text for details of the plumage scoring technique.

In 1990, on a diet supplemented with canthaxanthin, females from Michigan, Guerrero, San Jose, and Alviso all grew similar plumage with a wash of red on the rump, throat/breast, and crown (H = 2.45, df = 3, P = 0.49; Fig. 4). On a carotenoid-deficient diet, females from all four populations grew similar drab plumage with a wash of yellow on the rump and breast (H = 2.29, df = 3, P = 0.51; Fig. 4). After completing molt on a diet supplemented with canthaxanthin, females from all populations increased substantially in plumage brightness,

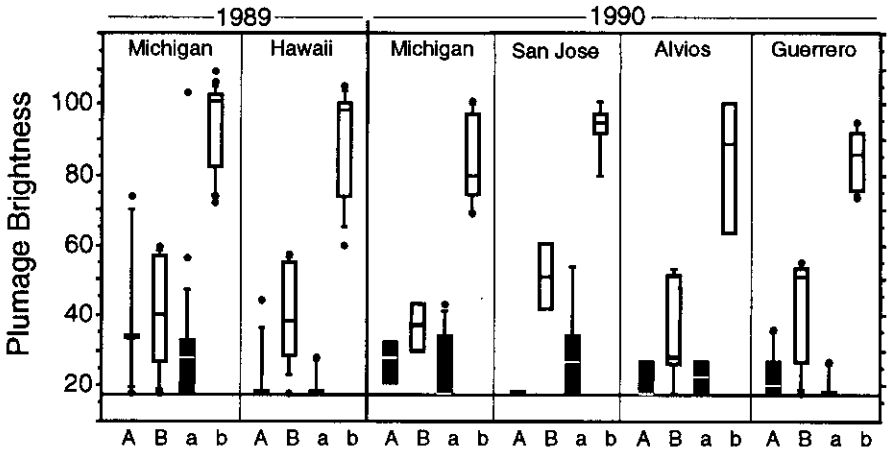

FIG. 4. Box plot of plumage brightness scores of captive female House Finches from various populations after captive molt on standardized diets in 1989 and 1990. Horizontal bars in box plots indicate the 10th, 25th, 50th, 75th, and 90th percentiles. Points give data for individuals outside this range. The bracketing horizontal line (plumage brightness = 18) indicates the score of females with no detectable carotenoid pigmentation. Solid bars are pretreatment scores; unshaded bars are post-treatment scores. A, pretreatment scores of females fed a plain seed diet; B, post-treatment scores of individuals fed a plain seed diet; *a*, pretreatment scores of females fed a diet supplemented with the red carotenoid, canthaxanthin; *b*, post-treatment scores of individuals fed a diet supplemented with canthaxanthin. See text for sample sizes and details of the plumage scoring technique and feeding experiments.

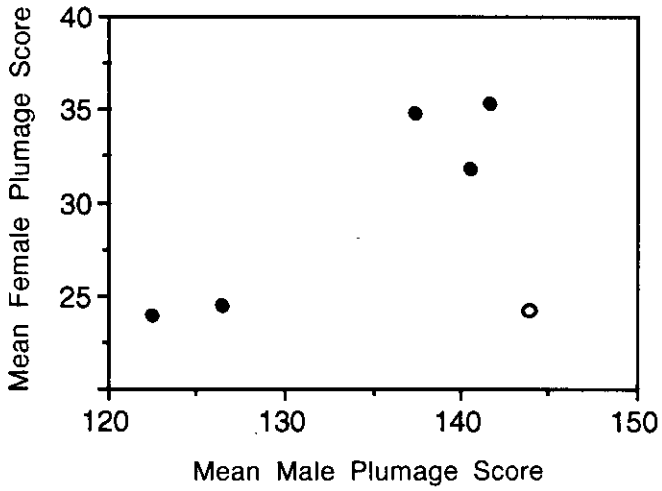

FIG. 5. The relationship between the mean brightness of male and female plumage among populations of *C. m. frontalis* (●) and *C. m. griscomi* (○).

with no overlap in pre- and post-treatment plumage brightness scores in any group (Fig. 4). Females from Alviso, San Jose, and Guerrero also increased substantially in plumage brightness score after completing molt on a plain seed diet, but the small sample sizes limited the power of the test for differences, and there was no significant difference in pre- and post-treatment scores for females from any population (Michigan: $z = 1.41$, $P = 0.16$; Alviso: $z = 1.84$, $P = 0.07$; San Jose: $z = 1.60$, $P = 0.11$; Guerrero: $z = 1.58$, $P = 0.11$; Fig. 4).

In 1989, I was able to determine the age of most Michigan females used in feeding experiments when they were captured. I found no significant difference in the plumage coloration of yearling and adult females after molt on either a diet supplemented with canthaxanthin ($n = 13$ and 16, respectively, $z = 1.55$, $P = 0.12$) or a plain seed diet ($n = 3$ and 13, respectively, $z = 1.71$, $P = 0.09$). In both comparisons, however, the trend was for yearling females to display brighter plumage, but the small sample sizes limited the power of these comparisons.

Relation to male brightness

Both male and female House Finches show substantial geographic variation in carotenoid plumage coloration. To look for a relationship between the relative brightness of males and females among populations, I regressed the mean plumage score of males from six populations (Michigan, New York Guerrero, Hawaii Island, Alviso, California, and San Jose, California) on the mean score of females from these populations. When all populations were considered, the relationship was not significant ($r^2 = 0.16$, $P = 0.23$); but when I included only *frontalis* populations in the comparison, I found a significant positive relationship ($r^2 = 0.81$, $P = 0.02$; Fig. 5). I also compared the proportion of females with detectable carotenoid pigmentation with the mean plumage brightness score of males. Again, the relationship was not significant when all populations were included ($r^2 = 0.29$, $P = 0.16$), but it was marginally significant when only *frontalis* populations were included ($r^2 = 0.64$, $P = 0.06$).

Discussion

When female House Finches are maintained on a common diet during molt, they all grow feathers with similar plumage coloration. Moreover, although many females in wild populations show no detectable carotenoid pigmentation, when they are provided with abundant red carotenoid pigments during molt all females grow plumage with red pigmentation on their rumps, undersides, and crowns, indicating that all females possess the capacity for such display. These observations suggest that, in the wild, differences in individual expression of coloration in females stem from differential access to carotenoid pigments during molt. Similarly, differences among populations in the mean coloration of females appear to result from regional differences in the availability of carotenoid pigments: no differences in female plumage brightness persisted among populations after females underwent captive molt on a

common diet. These findings, implicating dietary access to carotenoid pigments as the key determinant in intra- and interpopulation variation in expression of female plumage coloration, are very similar to previous observations regarding the control of carotenoid coloration in male House Finches (Brush and Power 1976; Hill 1992, 1993*b*).

Male and female House Finches are alike not only in the proximate control of expression of plumage coloration, but also in their patterns of geographic variation in plumage brightness. Among *frontalis* populations there is a significant positive correlation between the mean plumage brightness scores of males and females, which suggests that the sexes are similarly affected by regional and local variation in carotenoid availability. In contrast, however, *griscomi* males have a relatively high mean plumage brightness, while *griscomi* females show little ornamental coloration. This inconsistency in the relationship between the plumage scores of males and females may be explained by looking more closely at color display in *griscomi* males.

The *griscomi* population is exceptional not only for the difference in the mean coloration of males and females, but also for the very restricted ventral patches of coloration displayed by males (Moore 1939; Hill 1993*b*). I propose that these two features are related. Aviary studies indicate that *griscomi* males are more efficient at pigmenting their small ventral patches of coloration than are *frontalis* males at pigmenting their larger ventral patches: on the same canthaxanthin-supplemented diet, *griscomi* males grew feathers that were significantly brighter than those grown by *frontalis* males (Hill 1993*b*). Thus, the apparent inconsistency in the plumage brightness of *griscomi* males and females can be explained if the low plumage brightness score of *griscomi* females reflects a low availability of carotenoid pigments (as presumably do the low plumage scores of *frontalis* females from Hawaii and Alviso, California), but the small patches of *griscomi* males allow them to use small quantities of carotenoid pigments to achieve bright plumage.

This explanation for the pattern of color expression among male and female House Finches in different populations makes the implicit assumption that females do not actively forage for carotenoid pigments, while males do. Passive carotenoid intake by females is also suggested by the fact that even in areas where most males are bright red and where carotenoid pigments are likely abundant, a high proportion of females show no carotenoid pigmentation. Because male reproductive success is tied so tightly to successful garnering of carotenoid pigments (Hill 1990, 1991), one would expect male House Finches to maximize their intake of carotenoids. In the Cedar Waxwing, another species that has red carotenoid pigmentation of the plumage (Brush and Allen 1963) that functions in mate choice (Mountjoy and Robertson 1988), individuals show a significant preference for red foods during molt (McPherson 1988). On the other hand, sexual selection for expression of plumage coloration appears to be much weaker for female House Finches (Hill 1993*a*), while nutrient and calorie demand may be greater (in response to egg production and incubation). Consequently, it seems reasonable to suggest that female House Finches may forage to maximize their intake of calories or nutrients and only ingest carotenoids incidentally.

Passive carotenoid intake by females might also explain why the most colorful female House Finches tend to be yearlings (McEntee 1970; Fig. 4). Age effects disappeared when captive females were maintained on a common diet during molt (although the small sample size limited the power of this test), so there appear to be no intrinsic differences between yearling and adult females in the potential for color display. However, the commencement and duration of molt in yearling House Finches is more variable than in ASY individuals (Michener and Michener 1940). If the range of available food, and particularly the abundance of carotenoid pigments, changes throughout the molt period (see, for example, Slagsvold and Lifjeld 1985), then a relatively small difference in the timing of molt by adult and yearling females could account for the differences in expression of plumage coloration among these age groups. Yearling females that molt early or late in the season may tend to grow feathers in an environment that is richer in carotenoid pigments than that experienced by molting adults. In contrast, yearling male House Finches may tend to be less brightly plumaged than adult males (Michener and Michener 1931; Gill and Lanyon 1965; Hill 1992) because males, directly or indirectly, compete for carotenoid resources, and yearlings do relatively poorly in such competition (Hill 1992). Active foraging for carotenoid pigments by males may diminish the effect of seasonal variation in carotenoid availability.

In the Red-winged Blackbird (*Agelaius phoeniceus*), the only other dichromatic species in which female coloration has been studied in detail, the opposite age effect has been observed: ASY females tend to display brighter carotenoid pigmentation than yearling females (Payne 1969; Miskimen 1980*a*, 1980*b*; Blank and Nolan 1983). Like female House Finches, female Red-winged Blackbirds appear to be subject to weak sexual selection for color display (Muma and Weatherhead 1989), and the sexes differ markedly in the selection of food items during molt (data summarized in Miskimen 1980*b*), which suggests that females may not actively forage for carotenoid pigments. There is also some regional variation in the brightness of carotenoid coloration of female Red-winged Blackbirds that has been linked to regional differences in access to carotenoid pigments (Miskimen 1980*b*). However, in contrast to female House Finches, differences in the plumage brightness of yearling and ASY female Red-winged Blackbirds persist even when individuals are maintained on a common diet during molt (Miskimen 1980*a*, 1980*b*). This apparent intrinsic difference in the potential for color display by yearling and ASY females may be related to the fact that male Red-winged Blackbirds display a distinctive 1st-year plumage (Selander and Giller 1960) that involves both melanin and carotenoid pigmentation and is, at least partly, independent of diet (Greenwood 1985). These differences in the control of female coloration in House Finches and Red-winged Blackbirds illustrate the complexity and variability of expression of plumage coloration in dichromatic species.

An alternative explanation to the absence of active foraging by females is that females regulate their intake of carotenoid pigments in an adaptive manner. Winter dominance studies indicate that females generally supplant males from perches at feeders, even though males are larger (Thompson 1960; Brown and Brown 1988). Males may yield to females to increase their chances of pairing, or to improve the condition of prospective mates (Brown and Brown 1988); in this way drab females may gain access to more resources than bright females. If females did benefit by not displaying carotenoid pigmentation, females would be expected to avoid ingesting carotenoid pigments to remain drab. Yearling females may tend to ingest more carotenoid pigments than older females

because of inexperience, or other age-related factors. Passive versus selective carotenoid intake could be distinguished by food preference experiments and more detailed studies of winter dominance in relation to female coloration.

In this study I have shown that, like male House Finches, females show substantial variation in expression of carotenoid plumage coloration both within and among populations, and that yearling females tend to be more colorful than adult females. Feeding experiments suggest that local, regional, and age-related variations in plumage brightness are a result of differences in access to carotenoid pigments during molt. However, to adequately test both the idea that regional differences in the plumage brightness of females reflect regional differences in dietary access to carotenoid pigments, and that males and females differ in how actively they forage for carotenoid pigments, direct measures of the abundance of carotenoid pigments in the diets of males and females across environments are needed.

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